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R. C. L. Perkins' Legacy to Evolutionary Research on Hawaiian Drosophilidae (Diptera)[1]

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ABSTRACT: R. C. L. Perkins' influence on evolutionary research on the Hawaiian Drosophilidae is presented. His observations of the bizarre secondary sexual structures in this group led evolutionary biologists to focus research on the role of sexual selection in speciation and the evolutionary processes responsible for the proliferation of *Drosophila* species in the native Hawaiian fauna. A review of early taxonomic treatment of the group and some of the ecological novelties of the group are discussed. A better understanding of the genetics, ecology, behavior, morphology, etc. resulted in a revision of the generic concepts of the group, and subsequent phylogenetic studies using modern tools of molecular biology have confirmed the monophyletic relationships among the species in this group.

FROM 1893 TO 1897, R. C. L. Perkins conducted an extensive survey of Hawai'i's insect fauna. The results of Perkins' collections and the detailed field notes he recorded for the specimens including host records provided the basis for his publication in the *Fauna Hawaiiensis* (1913). Perkins' efforts and careful record keeping provide extremely valuable baseline information that we can use to infer relative abundance of the populations as well as the quality of the habitat in which these species lived a century ago. It will enable us to compare estimates of diversity in the insect fauna with surveys conducted during later decades especially in two groups that Perkins surveyed extensively: the *Megalagrion* damselflies and the platynine carabid beetles.

Although Perkins focused much of his efforts in collecting many of the groups of insects in Hawai'i, there were some groups that presented logistical problems for him primarily because of the difficult conditions fieldwork presented to entomologists of his time. It was clear that Perkins was "uncomfortable" with collecting dipteran species in the Hawaiian fauna. In his introduction to *Fauna Hawaiiensis,* he commented that ". . . the minute and obscure Diptera, the endemic species largely consisting of small Dolichopodidae, which shrink and distort on drying, and of infinite numbers of Drosophilidae, many of these also becoming distorted, have been little collected" (Perkins 1913). He had difficulty in preserving these soft-bodied insects under the harsh conditions he faced in the field and therefore he did not make a special effort to collect dipteran species as he did some of the other major orders of insects. Nevertheless, based on what he saw of the drosophilid fauna in Hawai'i, he made the following comments: "*Drosophila* is represented by an assemblage of species, exhibiting great diversity in structure and appearance. . . . At present these insects, many of which are obscure and minute forms, have been very imperfectly collected. To make an approximately complete collection and thorough study of the Hawaiian species would require the devotion of many years of special work. Not less than 250 species must exist in the islands, and double that number may very probably occur" (Perkins 1913:189).

Perkins recognized the tremendous diversity in the Drosophilidae, and his assessment of the group was echoed by Elwood C. Zimmerman, another entomologist with considerable experience in the Hawaiian fauna, who wrote a passionate plea to geneticists and evolutionists about the remarkable drosophilid fauna in Hawai'i and the opportunity to conduct "advanced research" on this group of flies. He

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said: "Since I became aware, many years ago, of the astonishing development of *Drosophila* in Hawaii, I have tried to interest geneticists and evolutionists in the fauna, but I fear that it has been considered, at least by some workers, that my descriptions of the size and diversity of the fauna are exaggerated. I do not exaggerate. It is possible that the Hawaiian drosophilid fauna may be the most remarkable in the world. In Hawaii is found a range from unusually small species to absolute giants up to one centimeter across, and there is much morphological diversity. There may be as many as 300 species concentrated in an area smaller than the little state of Massachusetts or less than one-fifth the size of Ireland. Where else has such a drosophilid fauna developed? Is this fauna not worthy of detailed attention by those equipped to do advanced research on the genetics and evolution of this group of fascinating flies?" (Zimmerman 1958:557).

Thus, Perkins' early observations of the Hawaiian Drosophilidae had an influence on the future evolutionary research of this group. In 1948, D. Elmo Hardy joined the Department of Entomology at the University of Hawai'i as a specialist on the systematics of fruit flies in the family Tephritidae. Although his primary research interests were in the tephritids of the Oriental and Pacific regions, as he began to collect flies from throughout the Hawaiian Islands, he came to the realization that the drosophilid fauna of Hawai'i was indeed a most remarkable group and that there was a tremendous opportunity to conduct intensive research on their biology. After Zimmerman's (1958) plea to geneticists and evolutionists to investigate the Hawaiian fauna, Hardy visited with Wilson S. Stone, director of the Genetics Foundation at the University of Texas at Austin, in 1962 and discussed the possibility of a joint research project between the University of Hawai'i and the University of Texas on the genetics and evolution of the Hawaiian Drosophilidae. Under the leadership of Stone and Hardy, proposals were prepared and submitted to the National Institutes of Health (NIH) and the National Science Foundation to study this group. The proposal to the NIH was successful in securing funds for 1 yr to support a team of researchers to obtain enough preliminary information on the Hawaiian *Drosophila* to justify continued funding for another 5 yr.

By the summer of 1963, Stone had assembled a team of researchers with expertise in nearly every aspect of evolutionary biology including taxonomy, morphology, ecology, behavior, cytogenetics, and developmental and molecular biology. Seven senior scientists from across the United States, plus Wilson Stone and Elmo Hardy as principal investigators, arrived in Hawai'i to launch a multidisciplinary research effort in answer to Zimmerman's plea to investigate the genetics and evolution of this remarkable fauna. That was the beginning of the so-called Hawaiian Drosophila Project (Spieth 1980). Since then, with continued funding support from the National Institutes of Health, the National Science Foundation, and other private organizations and foundations, nearly 80 senior scientists from all over the world have traveled to Hawai'i to investigate some aspect of the evolutionary biology of this group. In addition, more than 400 undergraduate and graduate students and postdoctoral fellows have participated in the project either as laboratory technicians or in conducting research on these flies as part of their educational curricula.

Brief History of the Taxonomy of the Hawaiian Drosophilidae

In 1952, Wheeler listed 73 species of drosophilids from the Hawaiian Islands, two of which were described by R. C. L. Perkins (1913), 45 by P. H. Grimshaw (1901–1902), and the rest by Knab (1914), Sturtevant (1921), Bryan (1934, 1938), Malloch (1938), Zimmerman (1938), and Wirth (1952). By the time of the start of the Hawaiian Drosophila Project in 1963, Hardy had already committed nearly 10 yr to naming and describing more than 300 new species of Hawaiian Drosophilidae and redescribing some of the species treated by his predecessors. His monograph on the systematics of this group was published in 1965 and listed 400 species in nine genera. Since then, Hardy (1966), Hardy and Kaneshiro (1968, 1969, 1971, 1972, 1975*a,b,* 1979), Kaneshiro (1969*b*), and Perreira and Kaneshiro (1990) have named and described another 111 species in the Hawaiian fauna. So, with a current total of 511 described species in the family Drosophilidae, it appears that Perkins' prediction of the number of species in this fauna may have been almost prophetic. However, a cursory inspection of the Hawaiian drosophilid collection at the University of Hawai'i indicates that there are still many more undescribed species in the fauna. It is estimated that there may be as many as 250–300 more undescribed species already in the collections and more new species are still being discovered as new collecting techniques are implemented and previously unsampled localities are studied. Kaneshiro (1993) estimated that 1000 species of drosophilids may be present in the Hawaiian fauna.

Although Hardy's (1965) treatment of the endemic fauna included nine genera, several lines of evidence indicated that the entire fauna can be separated into two major lineages: those included in the genus *Drosophila* and the remaining in the genus *Scaptomyza* (Throckmorton 1966, Kaneshiro 1976*a*). By pooling corroborating data from comparative studies of the internal anatomy (Throckmorton 1966), mating behavior (Spieth 1966, 1968), ecology (Heed 1968, 1971), and cytology of the metaphase and polytene chromosomes (Clayton 1968, Stalker 1970, 1972, Yoon et al. 1972), Kaneshiro (1976*a*), based on his comparative studies of the male genitalia, demonstrated that the "key" morphological characters used to differentiate the species into nine genera, although important for understanding phylogenetic relationships among species that shared those characters, were not valid for grouping species at the generic level. In an earlier paper, Kaneshiro (1969*a*) showed that speciation in the Hawaiian drosophilids (especially that of the picture-winged group) resulted in tremendous morphological diversity, but with remarkable stability in the structures of the male genitalia. He showed that the male genitalic apparatus could be used as an important tool for demonstrating phylogenetic relationships among species in this group and that the relationships derived from such data correlate closely with the phylogenies derived from chromosomal relationships (Carson et al. 1970, Carson 1971*a*, Clayton et al. 1972).

Kaneshiro (1976*a*) suggested that the conventional morphological characters used by Diptera taxonomists were not valid as generic characters and, in fact, could give a misleading impression of evolutionary divergence in the Hawaiian fauna. It was shown that the so-called "key" generic characters were secondary sexual structures of the males that were used in the complex courtship displays observed in these species. Females lacked these structures and for the most part could not be differentiated from typical *Drosophila* species. Thus, species previously placed in separate genera proved to be nothing more than species groups within the genus *Drosophila*. The endemic genus "*Idiomyia*" (Grimshaw) had already been sunk as a synonym of *Drosophila* (Hardy and Kaneshiro 1968), and Kaneshiro (1976*a*) sank the three remaining endemic genera, *Antopocerus, Nudidrosophila,* and *Ateledrosophila* (listed in Hardy's [1965] monograph) as synonyms of the genus *Drosophila*.

Ecology of the Hawaiian Drosophilidae

Drosophila melanogaster (Meigen), a species commonly used by geneticists for a multitude of laboratory studies, has been given the common name "fruit fly." However, for many other *Drosophila* species, especially those from Hawai'i, "fruit fly" is a misnomer that should be avoided because of the confusion with fruit fly species in the family Tephritidae, which are important agricultural pests. In Hawai'i, *Ceratitis capitata* (Wiedemann) (the Mediterranean fruit fly), *Bactrocera dorsalis* (Coquillett) (the oriental fruit fly), *Bactrocera curcurbitae* (Coquillett) (the melon fly), and *Bactrocera latifrons* (the Malaysian fruit fly) are serious agricultural pests and there have been numerous discussions about statewide eradication of these species. It is important that the general public not confuse the two groups and misunderstand the conservation significance of the native Hawaiian drosophilids.

Perkins' (1913) observations on the breeding ecology of these species laid the groundwork for future ecologists on the Hawaiian Drosophila Project. He noticed that Hawaiian *Drosophila* species utilized a variety of hosts as larval breeding substrates. ". . . Some of the species are quite conspicuous, and are readily attracted by the sap oozing from a broken limb of a tree, or from exudations caused by decay or disease. Very many breed in stems of trees or plants, which, when decaying, yield abundant moisture, such as those of the arborescent lobelia, of banana, tree ferns, etc." (Perkins 1913:189). Indeed, decaying leaves and branches of the lobelia group in Hawai'i have been found to be extremely important larval breeding substrates for many of the Hawaiian *Drosophila* species. Although Perkins reported that bananas served as a breeding substrate, it is not likely that the endemic species utilized bananas as their larval host, and certainly fresh bananas are never used (even by nonnative drosophilids) as larval breeding sites.

During the first decade of the Hawaiian Drosophila Project, the research focus was to get a better idea of the basic biology of this remarkable group. Information on the ecology (Heed 1968, 1971, Montgomery 1975) and behavior (Spieth 1966, 1968) of the group did not rely on the ability to rear these species in the laboratory, but the results of this research contributed substantially to the success of subsequent research on this group. When the Hawaiian Drosophila Project began in 1963, the first major stumbling block to detailed genetic and evolutionary studies of the group was the difficulty in rearing and maintaining laboratory colonies, and continued funding for the project was very much dependent on our ability to establish laboratory colonies of these species. The work of Heed (1968, 1971) and Montgomery (1975) showed that most of these flies were host specific (i.e., the larval breeding substrate for each species was restricted to a single host plant in the native ecosystem). It turned out that host specificity was tied not to the nutritional requirements of the larvae but rather to the ovipositional behavior of the females (unpubl. obs.). By understanding the natural host plant on which these flies oviposited, it was possible to provide either small pieces of the decaying parts of these host substrates or a water extract of this material (a *Clermontia* or *Cheirodendron* "soup" for example) to stimulate the females to oviposit. Once the eggs were laid and hatched, the larvae fed and completed development on the artificial medium that had been developed especially for the Hawaiian *Drosophila* (Wheeler and Clayton 1965). The ecological data provided critical information about the specific substrate requirements to stimulate females to oviposit in the laboratory, and many species were raised at least to the F_1 generation to obtain the cytological data (Carson 1966, 1969, 1971*a,* Clayton 1966, 1968, 1969, 1971, Carson and Stalker 1968*a,b,c,* 1969, Stalker 1970, 1972, Yoon et al. 1972), which required rearing larvae until the third instar. Some species were maintained as standard laboratory colonies that could be hybridized with related species for genetic studies of reproductive isolation, or for behavior studies when it was necessary to obtain virgin females for mate preference experiments, for example.

Not only were the Hawaiian drosophilids found to be specialists on different host plants in the native ecosystem, it was also found that many species were specific on different parts of the plant (see Heed 1968, 1971, Montgomery 1975). For example, some species utilized decaying leaves ("leaf-breeders") of native trees and shrubs; others utilized the decaying bark or branches ("bark-breeders") of these plants as larval breeding substrates. Other species bred in the flowers of morning glory plants and those of the endemic silversword species. Still others were found to be specific on the different kinds of fungi and mushrooms ("fungus-feeders") that were found in the native rain forests. The *hawaiiensis* subgroup of the picture-winged species group lay their eggs on the slime flux of native trees such as *Acacia koa* or *Myoporum sandwicense.* One group of Hawaiian drosophilids, in the *Scaptomyza*-related genus *Titanochaeta,* has turned to predatory behavior, laying their eggs on egg masses of an endemic spider in the family Thomisidae, with development of the immature stages being completed entirely within the egg masses of these native spiders.

In addition to the wide range of larval breeding substrates, the Hawaiian Drosophilidae inhabit the entire range of habitats found in the native ecosystem. Species can be found in dry forests on the leeward sides of the Islands with less than a few centimeters of rainfall per year, and others can be found in deep rain forest habitats on the windward sides of the Islands where a few hundred centimeters of rain may fall per year on the average. There may even be a drosophilid species that has invaded the aquatic habitat. Several years ago, when a couple of Hawaiian *Drosophila* researchers were hiking through the backcountry of the North Kohala Mountains on the island of Hawai'i, attempting to reach forested areas to sample for drosophilid species, they came across a stream where adults of a drosophilid species were observed sitting on large boulders in the middle of the stream. After several minutes of searching, they discovered larvae that, under a 10X hand lens, appeared to be those of a drosophilid inhabiting the green algae scraped from below the surface of the water. Plastic bags were used to collect a sample of the stream water and green algae containing the larvae and transported to the laboratory at the University of Hawai'i on the island of O'ahu in an attempt to rear out the adults to confirm that the larvae were those of the drosophilid adults sitting on the boulders. Unfortunately, all of the larvae suffocated and none survived the trip back to the University campus where aerators could have been used to keep them alive until pupation and eclosion of the adults. Nevertheless, indications are that at least one Hawaiian drosophilid species may have invaded the aquatic habitat (pers. obs.).

Speciation in the Hawaiian Drosophila

Once the basic biologies were understood for those species that could be cultured in the laboratory, more detailed analyses of speciation mechanisms and evolutionary processes were possible. One group of species, the picture-winged group, became the primary focus of investigation during the first three decades of the project as researchers began to investigate the genetics of the speciation process. The group comprises 111 species that are mostly large-bodied with striking maculations on the wings that vary from species to species. This group was extremely well suited for these studies because many of the species could be reared in the laboratory, and detailed analyses of their morphology, behavior, genetics, cytology, proteins, and DNA could be conducted. The banding patterns of the giant polytene chromosomes extracted from the salivary glands of the third instars were especially favorable for comparative studies, allowing Carson and his colleagues to conduct extensive surveys of the inversion patterns of most of the species in this group (see Carson [1987] and [1992] for reviews).

Carson's (1968, 1971*b,* 1974, 1975) work on the phylogenetic relationships of the picture-winged species based on the chromosomal inversion patterns enabled him to formulate his founder event theory of species formation in the Hawaiian fauna. Spieth's (1966, 1968) early studies on the elaborate courtship behavior of a wide range of species showed that the oftentimes bizarre secondary sexual structures were a critical ingredient in the speciation process of these species. Based on Spieth's observations of the complex mating system in these flies and the potential role that sexual selection might have played in species formation, Kaneshiro (1976*b*) conducted a series of mate-preference experiments among four of the picture-winged species. Based on the results of these experiments, he formulated a mechanistic model in which sexual selection was portrayed as a truly dynamic system (Kaneshiro1987). It was suggested that at small population size such as during the initial stages of colonization following the founder event, there might be shifts in the distribution of mating types in the population because there would be strong selection against those females that were highly discriminating in mate choice. Under those conditions, there would be an increase in the frequency of less-discriminating females because these would be the females most likely to contribute genetic material to the next generation. Substantial changes in the genetic background of the population as a result of the shift in gene frequencies that accompanies the shift in the distribution of mating types may promote the genetic revolution (Mayr 1963) or genetic transilience (Templeton 1980) that has been associated with founder-event speciation models. The dynamics of the sexual selection system appears to have played an important role during the initial stages of the speciation process and provides the mechanism for the generation of novel genetic recombinants upon which the forces of natural selection can act (Kaneshiro 1989). Thus, shifts in the mating system and the corresponding destabilization of the genetic environment that accompany founder-event colonization can be synergists for species formation.

The Evolution and Development of Secondary Sexual Structures

Perkins, more than 80 yr ago in his paper in the *Fauna Hawaiiensis* (1913:65), made the following observation: "it is interesting to observe in animals in which secondary sexual characters of the male are conspicuous, that when geographical isolation has taken place, these are generally modified, in fact herein may apparently be the only modifications, as if these sexual characters were often the first to become changed."

It is clear to researchers of the Hawaiian *Drosophila* that sexual selection has indeed played an important role in the speciation and evolution of this group. The oftentimes bizarre secondary sexual structures observed in the males of Hawaiian *Drosophila* species are manifestations of the complex courtship and mating behaviors (Figure 1) that have driven the speciation process.

Much of the earlier work on the Hawaiian Drosophila Project involved the picture-winged species group, which could be reared relatively easily in the laboratory to enable various experiments requiring laboratory colonies and the availability of large numbers of individuals of each species. With the development of the molecular biology and DNA sequencing technologies, we are beginning to turn some attention to the other species groups that are more difficult to rear and maintain in the laboratory and for which only a few individuals can be collected from nature. As indicated above, some of the other species groups had evolved secondary sexual structures that were so divergent from typical drosophiloid characters that they were separated into different genera. For example, the antennae of the males of the former genus *Antopocerus* bear an enlongated, whiplike arista with shorter, dense hairs on the dorsal and ventral surfaces (Figure 2*a*). This is contrasted to the long dorsal and ventral rays on the arista of the females' antennae, which are more typical of drosophiloid species (Figure 2*b*). Also, the front legs, especially the tarsal segments of antopocerus species, are often embellished with long hairs and sometimes with a shortened second tarsal segment (see Figure 3*a*), compared with the tarsal segments of a more typical drosophiloid leg as can be observed in the females of the antopocerus species (Figure 3*b*). Furthermore, Kaneshiro (1976*a*), in a revision of the generic concepts of the Hawaiian Drosophilidae, showed that the male genitalia of the antopocerus species could not be readily distinguished from those of the modified-tarsus group in the genus *Drosophila* and that there were close affinities between the two groups. Thus the genus *Antopocerus* was sunk as no more than a species group related to the modified-tarsus group in the genus *Drosophila* (Kaneshiro 1976*a*).

The secondary sexual structures that charac-

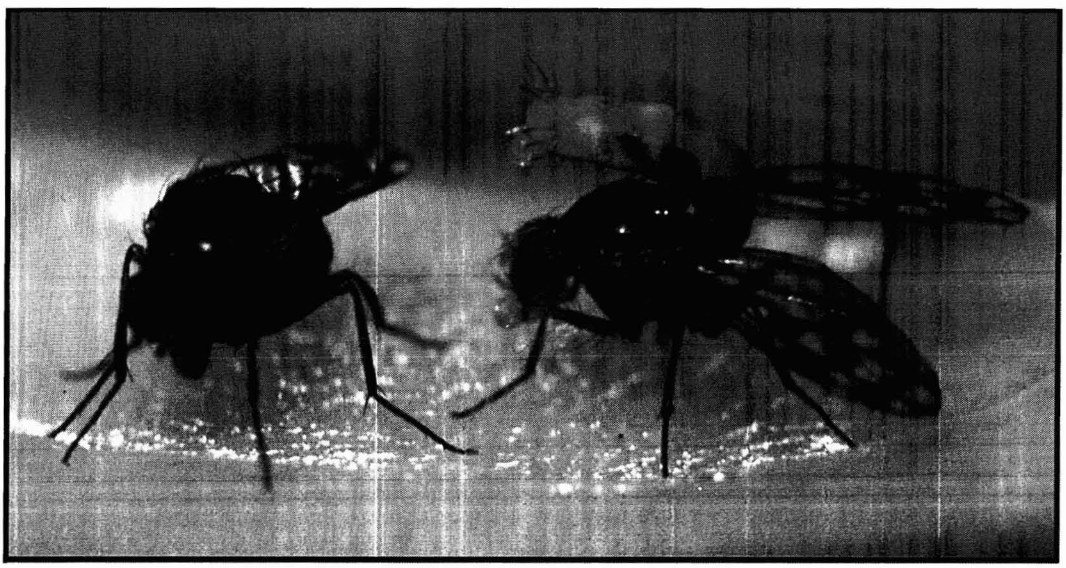

FIGURE 1. Courtship display of *D. clavisetae* with male (*right*) curling his abdomen up and over his head, producing a bubble of sex pheromone from the terminalia.

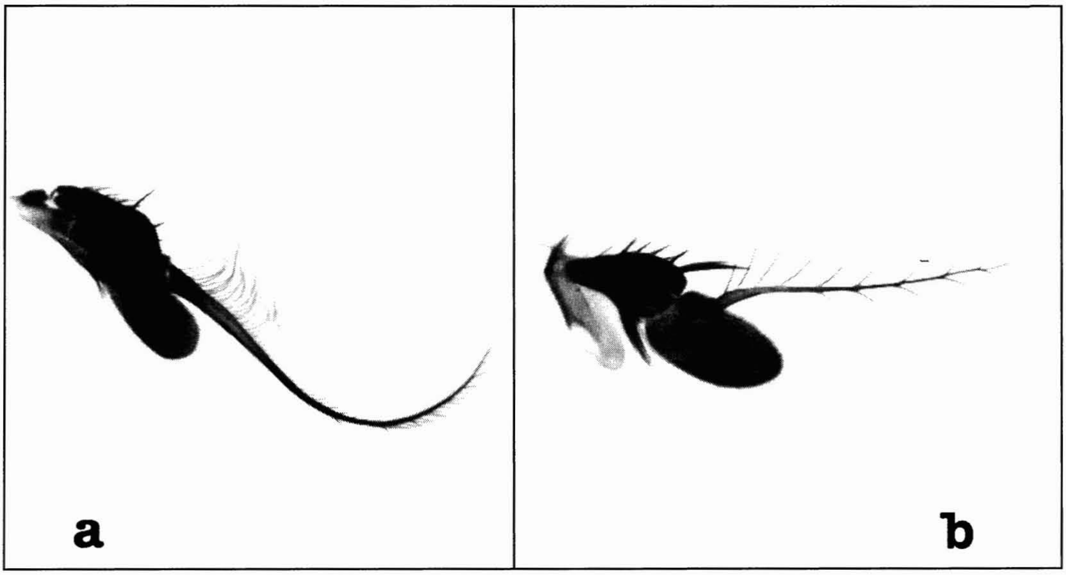

FIGURE 2. Antennae of antopocerus species: (*a*) male, (*b*) female.

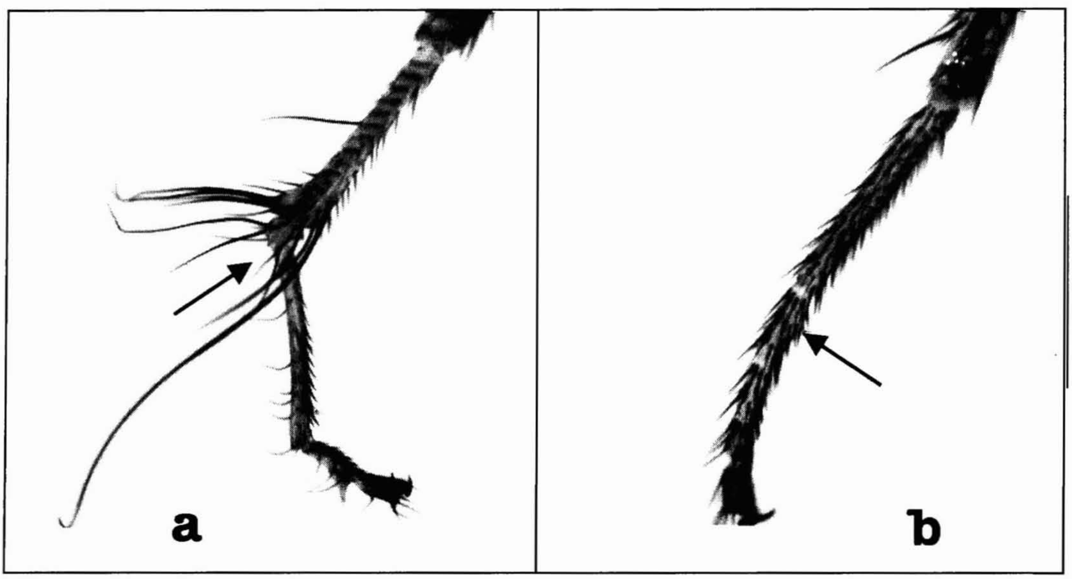

FIGURE 3. Tarsal segments of forelegs of antopocerus species: (*a*) male, (*b*) female.

terize groups of species can sometimes be found in what appear to be unrelated species based on other morphological characters. For example, Carson's chromosomal phylogeny of the picture-winged species group is rooted by two species from the island of Kaua'i, *D. primaeva* and *D. attigua*. Neither of these species is considered a typical picture-winged species because they both lack distinct markings on the wings, but based on comparative studies of the giant polytene chromosomes they can be shown to be close to the ancestral base of the picture-winged group.

Nor are they considered to be typical of the fungus-feeder group, where the species are typically slender-bodied and shiny black in body coloration, whereas both *D. primaeva* and *D. attigua* are heavy-bodied and reddish brown. Nevertheless, these latter species have a characteristic black rim on the apex of the labellum (Figure 4*a*), a feature that is used to characterize the fungus-feeder group (Figure 4*b*). The shared character suggests a close affinity of the fungus-feeder group to the *D. primaeva* subgroup of the picture-winged chromosomal phylogeny.

Some picture-winged species in the *D. adiastola* subgroup also have striking modifications in their mouthparts, with strong spines (see Figure 5 for example) similar to what may be seen in the large and heterogeneous "modified mouthparts" species group. Furthermore, there is a characteristic bristle near the apex of the fore femur (Figure 6*a*) in males of a group of modified-mouthpart species, the *D. comatifemora* subgroup. This same feature is also present in the males of all of the species of the *D. adiastola* subgroup (Figure 6*b*).

Thus, by making detailed comparative studies of these secondary sexual structures combined with comparative analyses of the structures of the external male genitalia, especially that of the aedeagus, it may be possible to infer phylogenetic relationships among the Hawaiian Drosophilidae. The fungus-feeder group is suggested as a group near the ancestral progenitor of the Hawaiian Drosophilidae, with close affinities to the *D. primaeva* species group. When one examines the "sclerotized" black rim on the labellum of the fungus-feeder species under high magnification, what appears to be "sclerotization" is a row of densely appressed bristles (unpubl. obs.). It is postulated that a relatively simple genetic change (mutation) could have led to the development of the kind of modifications seen in the labellum of the modified-mouthparts group (see, for example, the modified mouthparts of *D. ornata* in Figure 5), which may have served as progenitors of the picture-winged group and the other species groups that share similar characteristics of the male genitalia (Kaneshiro 1969*a*, 1976*a*).

With the advancement of developmental and molecular biology technologies, we plan to use these new tools to investigate the evolution of the secondary sexual characters in the Hawaiian *Drosophila*. It is hoped that these studies will provide further insights into the evolution of the

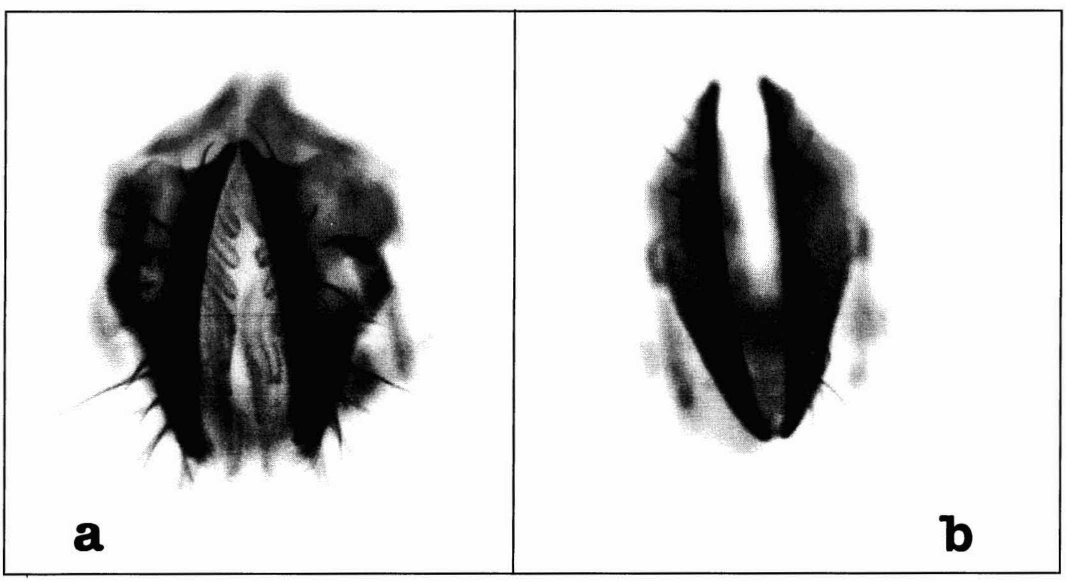

FIGURE 4. Ventral view of mouthparts of *(a) D. primaeva* and *(b) D. nigra,* a fungus-feeder species showing black-sclerotized rim on the apex of the labellum.

FIGURE 5. Lateral view of labellum of *D. ornata,* a picture-winged species in the *adiastola* subgroup.

sexual selection system that has resulted in the development of some of the bizarre secondary sexual structures so characteristic of the Hawaiian drosophilids.

The Hawaiian Drosophilidae and Conservation Biology in Hawai'i

In a review of the Hawaiian Drosophila Project prepared by the National Science Foundation in 1976, the project was cited as one of the best examples of multidisciplinary approach to biological investigation. Hampton L. Carson, one of the first to arrive in Hawai'i as a member of the Hawaiian *Drosophila* research team, in an interview with Ed Edelson (1985), stated that the opportunity to match genetic, behavioral, and morphological studies in an area of rapid speciation makes Hawai'i, in Carson's words, "God's gift to the evolutionist."

But Hawai'i's native ecosystems are threatened by a number of things, including the destruction of native forests for agriculture and for other economic reasons and the invasion of alien species that compete with native species for limited resources. The ubiquity of the Hawaiian Drosophilidae in a wide range of native Hawaiian habitats makes the group a potential indicator group for monitoring the health of native Hawaiian ecosystems. The more than three decades of field records and an understanding of the group's association with the native ecosystems, as well as host specificity on endemic plants, provide a strong database upon which long-term monitoring programs can be developed for assessing the stability of some of the most critical habitats for rare and endangered plant and animal species in the Hawaiian Islands. As more of the undescribed species of Hawaiian Drosophilidae are treated taxonomically and more biological information is obtained for these species, the group will become increasingly more valuable as potential indicator species for conservation biology in Hawai'i. As stated by Mark Williamson in his book *Island Populations* (1981:196), "Of all the groups of organisms, plants or animals,

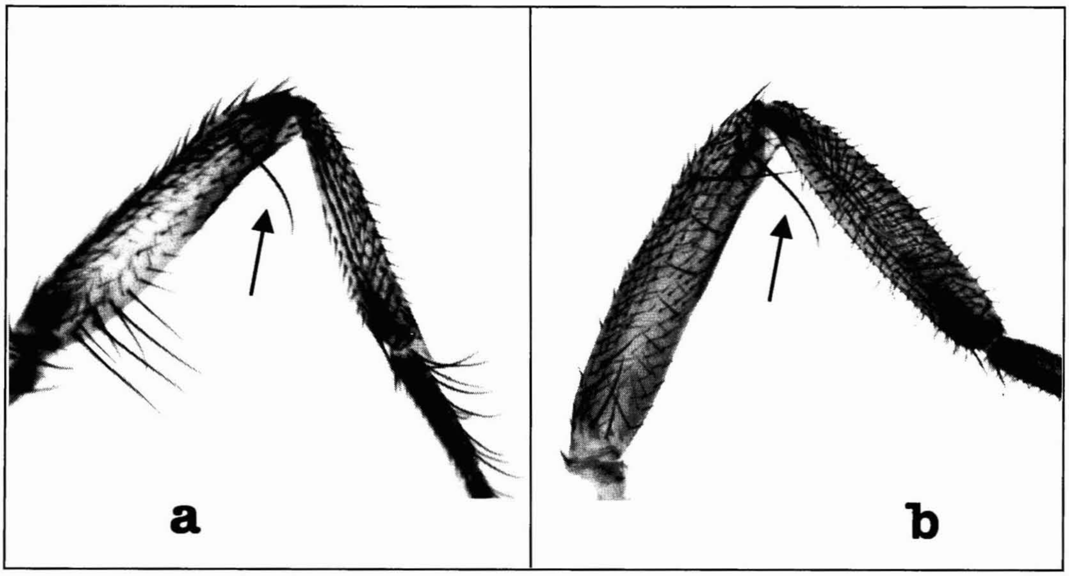

FIGURE 6. Forelegs of *(a) D. comatifemora,* a modified-mouthparts species, and *(b) D. ornata,* a picture-winged species, showing strong curled bristle near the apex of the femur.

that can be studied on islands, the Hawaiian Drosophilidae are supreme. . . . There is still an immense amount of work to be done on the group, but the work carried out so far clearly establishes their supremacy."

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